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Leaf litter microbial decomposition in salinized streams under intermittency

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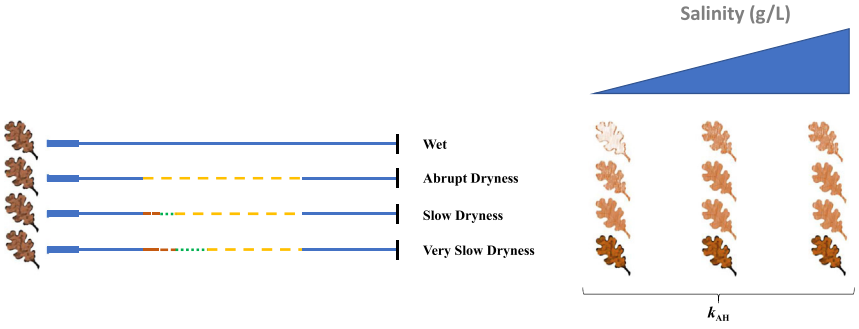
HIGHLIGHTS

- Stream salinization effects on streams may be intensified by drought events.
- Salt addition reduced the biomass and eliminated the sporulating capacity of fungi.
- Energetic trade-offs may maintain fungal efficiency under salt contamination.
- Drought patterns differentially affect fungal mediated decomposition.
- Abrupt drought affected the structure and composition of the fungal communities.

GRAPHICAL ABSTRACT



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ABSTRACT

Human-induced salinization of freshwaters constitutes a growing global problem, whose consequences on streams functioning are largely unknown. Climate change projections predict enhanced evaporation, as well as an increase in extreme events and in variability of precipitation. This will result in more frequent, extended and severe drought periods that may aggravate water salinization of streams and rivers. In this study we conducted a microcosm experiment to assess the combined effects of three drought regimes - abrupt (AD), slow (SD) and very slow transition to dryness (VSD) - and three levels of salinization (0, 4, 6 g L^{-1} NaCl) on microbial-mediated oak leaf decomposition over ten weeks. Salinization did not affect mass loss and associated microbial respiration of colonized oak leaves but significantly reduced the biomass and eliminated the sporulating capacity of fungi. Desiccation negatively affected leaf decomposition regardless of regime. Even though microbial respiration did not react to the different treatments, lower fungal biomass, diversity, and conidial production were observed under AD; for fungal biomass these effects were amplified at higher salt concentrations (particularly at 6 g L^{-1}). Our results indicate that effects of leaf litter desiccation depend on the rate of transition between wet and dry conditions and on the level of salt in the water. The two factors jointly affect decomposer survival and activity and, by extension, the dynamics of detrital food webs in streams.

1. Introduction

Freshwater salinization is a global, yet still understudied, threat to the ecological status of streams and rivers (Schäfer et al., 2012; Cañedo-Argüelles et al., 2013; Szöcs et al., 2014). Its intensification and geographical expansion, particularly in semi-arid and Mediterranean areas

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(Cañedo-Argüelles et al., 2013; IPCC, 2014; Kefford et al., 2016), parallels human population growth, which leads to higher water demand and extended anthropogenic activities (e.g. agricultural irrigation, mining and industrial activities, or the use of salts as chemical deicing and anti-icing agents), and accelerates global warming (IPCC, 2014; Kaushal et al., 2018; Cañedo-Argüelles et al., 2013, Cañedo-Arguelles et al., 2016; Tyree et al., 2016). Greater salt concentrations in streams may be expected by the increase evaporative concentration promoted by higher air temperatures. Climate change is also projected to cause more frequent extreme events including periods of severely reduced precipitation and enhanced evaporation, resulting in more frequent, extended and severe droughts (Trenberth et al., 2013; Pekel et al., 2016). These changes may push streams to cross the cease-to-flow threshold, causing a disruption of stream hydrological connectivity and, in extremis, the temporary loss of aquatic habitat (Acuña et al., 2005). The additional stress of intermittency may aggravate water salinization in stream ecosystems (Dieu Hien et al., 2018; Olson, 2018).

Small forested streams are light-limited systems energetically fuelled by detritus supplied by their riparian areas. Litter decomposition is the crucial ecosystem process that controls organic matter processing and nutrient cycling (Wallace et al., 1997; Wipfli et al., 2007). Decomposition is driven by the concerted action of microbial decomposers (primarily aquatic hyphomycete fungi; AH), which stimulates leaf litter consumption by invertebrates and detrital incorporation into secondary production (Canhoto and Graça, 2008). The decomposition process is biologically dominated but dependent on stream environmental factors that may affect the rates, the dynamics and the relative importance of the involved biota (Krauss et al., 2011). Information on the effects of salinization vs other stream stressors (e.g. nutrients, metal contamination) on litter decomposition is comparatively scarce; existing data emphasize inhibition of decomposition rates (Schäfer et al., 2012; Cañedo-Argüelles et al., 2013, 2014) dependent on the intensity and frequency of salt inputs as well as on baseline tolerance and efficiency of the invertebrate community (Horrigan et al., 2005, 2007; Cañedo-Argüelles et al., 2012; Kefford et al., 2016). Recent findings indicate that AH species are generally more tolerant to salt than invertebrates and guarantee litter processing at high levels of salinization (e.g. up to 4 g L^{-1}; Canhoto et al., 2017). They even maintain (less efficient) leaf degradation, driven by an impoverished community tolerating salt levels lethal to most stream invertebrates (e.g. Byrne and Jones, 1975; Sridhar and Kaveriappa, 1988; Kefford et al., 2012, 2016; Cañedo-Argüelles et al., 2014; Canhoto et al., 2017). Fungal resilience in short or long-term salt-contaminated streams seems to be based on energetic trade-offs among fungal requirements for hyphal growth, conidial production, and potential investment in metabolic and/or physiological tolerance (Canhoto et al., 2017; Gonçalves et al., 2018). Correlations between the effect of salt on fungal decomposition and other biological endpoints such as fungal biomass and diversity, or microbial respiration, are not straightforward and need to be clarified (Schäfer et al., 2012; Cañedo-Argüelles et al., 2014; Gómez et al., 2016; Sauer et al., 2016; Canhoto et al., 2017).

Our capacity to forecast the effects of salinization on stream functioning is still embryonic and further complicated by potential interactions with other stressors and environmental contexts. Drought events, in particular, are an increasingly common feature of a large number of headwaters in areas where anthropogenic salinization prevails. While the effects of flow disruption on streams functioning is most commonly linked to a lower density and diversity of invertebrates (Corti et al., 2011; Datry, 2012; Arroita et al., 2014; Chessman, 2015; Chester et al., 2015; Piniewski et al., 2016; Stubbington et al., 2016), the negative impact of various flow intermittency scenarios (duration, intensity and frequency) on litter decomposition has also been associated with reduced activity and diversity of microbial decomposers (Maamri et al., 2001; Bruder et al., 2011; Schlief and Mutz, 2011; Foulquier et al., 2014; Gonçalves et al., 2016; Duarte et al., 2017; Arroita et al., 2018). Nonetheless, recent studies suggest that the plasticity and resilience of some fungal species may guarantee leaf processing after resumption of stream flow, provided no severe and/or long-lasting interruption has occurred (Bruder et al., 2011; Gonçalves et al., 2016; Duarte et al., 2017; Arroita et al., 2018). In the latter case, the deleterious legacy of drought (essentially when it caused extinction of functionally dominant fungal species) on stream ecosystem functioning may be long-lasting and persist when flow is restored (Bruder et al., 2011; Gonçalves et al., 2016; Duarte et al., 2017; Arroita et al., 2018).

To our knowledge no study has assessed the combined effects of salinization and drought on microbial-mediated leaf decomposition. Considering the potential key role of the fungal compartment in the functioning of salinized streams (Canhoto et al., 2017) and in intermittent watercourses (Bruder et al., 2011; Gonçalves et al., 2016; Duarte et al., 2017; Arroita et al., 2018) this represents crucial information for protecting streams and maintaining their ecological services, particularly under global change scenarios (Suárez et al., 2017).

In the present study we conducted a microcosm experiment to assess the combined effects of salinization (0–6 g L^{-1} NaCl) and intermittency regimes (abrupt, slow and very slow transition to dryness) on fungal-mediated leaf litter decomposition and associated metabolic descriptors. We hypothesized that both stressors would induce significant changes in decomposition efficiency of AH; an expected lower decomposition rate may be connected to decreased fungal metabolic activity, and consequent severe reduction on reproductive and growth capacity. Negative effect of salinity would be potentially amplified by drought, with a fast rate of transition between wet and dry conditions inducing a stronger impact on fungal community performance. Accordingly, we also predict that stream intermittency would exacerbate stream community responses to the presence of salt, preventing an eventual functional recovery from extreme events (higher salinity together with abrupt drought) after rewetting.

2. Material and methods

2.1. Experimental setup

Senescent oak leaves (*Quercus robur* L.) were colonized in a reference oligotrophic permanent stream (i.e. Ribeira de S. João, Central Portugal) for 1 week (w). Fine mesh bags (10 × 15 cm, 0.5 mm mesh) were filled with oak leaves previously collected immediately after abscission and air-dried in the dark, at room temperature, in the laboratory.

After fungal colonization, sets of twenty leaf discs were punched out with a cork borer (12 mm diameter) and randomly distributed into 100 mL Erlenmeyer flasks containing 40 mL of nutrient solution (75.5 mg $CaCl_2$, 10 mg $MgSO_4 \cdot 7H_2O$, 0.5 g 3-morpholinopropanesulfonic acid (MOPS), 5.5 mg K_2HPO_4 and 100 mg KNO_3 per liter of sterile distilled water; Dang et al., 2005) enriched with salt to expose them to a gradient of salinization (0, 4 and 6 g L^{-1} of NaCl). The choice of 4 g L^{-1} of NaCl was based on Canhoto et al. (2017), where this concentration has shown to be a critical threshold, above which the fungal growth, conidium production and decomposing capacity of several AH species may be affected. 6 g L^{-1} was observed in a long-standing salted stream in Portugal (Ribeira de Pontével). The experimental period in the laboratory lasted 10 w, with the respective medium being renewed every 2 days during the immersion periods. All microcosms were incubated at 18 °C (common summer water temperature before drought events) and aerated on an orbital shaker (100 rpm unless otherwise specified) under 12 h light: 12 h dark photoperiod conditions, and subjected to the following four intermittency treatment (Fig. 1):

- Wet (W) - permanent immersion period in lab microcosms for 10 w (3 [salt] × 3 replicates = 9 microcosms);
- Abrupt Dryness (AD) - after 2 w immersion in the lab, the discs were subjected to 5 w of complete dryness (removing all of the medium

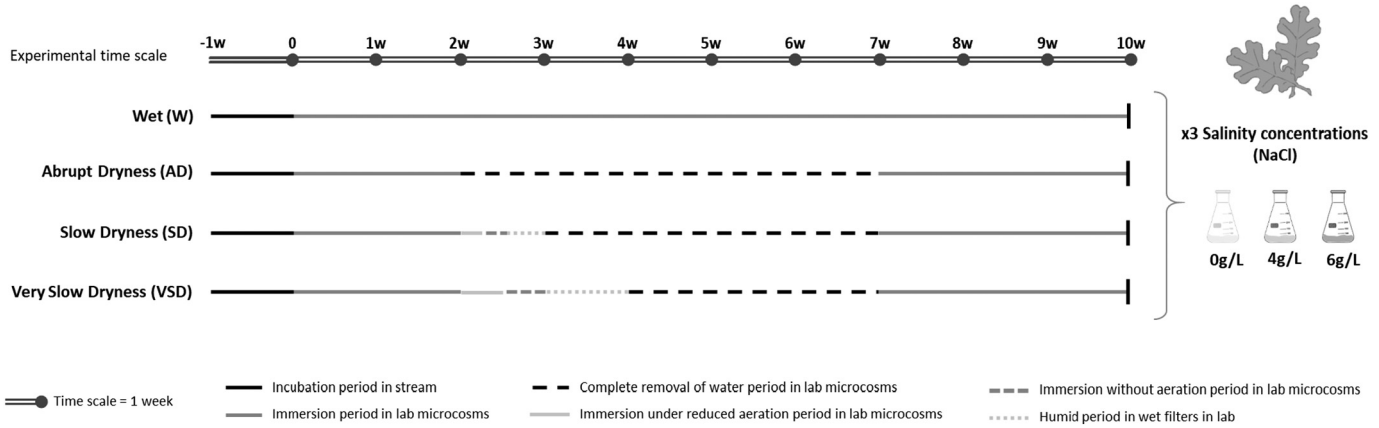

Fig. 1. Experimental design. Oak leaf discs were incubated in stream for 1 w, and then incubated in microcosms in the lab for 10 w. Microcosms were exposed to four intermittency regimes (W - wet, AD - abrupt dryness, SD - slow dryness and VSD - very slow dryness) at three salinity concentrations (0, 4 and 6 g L^{-1} NaCl).

and exposing discs to air inside the Erlenmeyer flasks); 3 w of re-soaking in the corresponding salted nutrient solution following the dry period. This treatment simulates the abrupt and complete disappearance of water in intermittent streams in summer (3 [salt] × 3 replicates × 3 sampling dates = 27 microcosms) followed by resumption of water flow;

- Slow Dryness (SD) - after 2 w immersion in the lab, the discs of each microcosm were subjected to a gradual exposure to dryness for 1 w (i.e., 2 days immersion under reduced aeration at 50 rpm + 2 days immersion without aeration at 0 rpm + 3 days exposed to a humid environment, discs in contact with a permanently wet filter paper), followed by a complete dryness for 4 w (exposed to air and without contact with water), and a 3 w re-soaking in the corresponding salted nutrient solution. This treatment simulates a gradual drought in intermittent streams in summer (3 [salt] × 3 replicates × 2 sampling dates = 18 microcosms) followed by resumption of water flow;
- Very Slow Dryness (VSD) - after 2 w immersion in lab, the discs of each microcosm were subjected to an elongated exposure to dryness for 2 w (i.e., 4 days immersion under reduced aeration at 50 rpm + 4 days immersion without aeration at 0 rpm + 6 days exposition to a humid environment, discs in contact with a permanently wet filter paper), followed by a complete dryness for 3 w (exposed to air and without any contact with water), and a 3 w re-soaking in the corresponding salted nutrient solution. This treatment simulates a very slow transition to drought in intermittent streams in summer (3 [salt] × 3 replicates × 2 sampling dates = 18 microcosms) followed by resumption of water flow.

These wet-dry duration periods were based on Bruder et al. (2011) and Gonçalves et al. (2016), to ensure that oak leaf discs were completely air dried and that fungal species were reactivated by re-soaking.

After incubation in the lab, all microcosms were sacrificed to evaluate leaf mass loss, microbial respiration, sporulation rate and total fungal biomass.

2.2. Leaf mass loss

After the initial incubation period in the stream (1 w) ten additional sets of twenty leaf discs were used to determine average initial dry mass (DMi) before the lab incubation period; we assumed this average as the DMi of all microcosms to determine subsequent mass loss at each treatment.

In all cases, at the end of 10 w incubation in the lab, dry mass loss (% DM) was estimated as the difference between the initial (DMi) and the final dry mass (DMf) of the twenty leaf discs from each microcosm.

2.3. Total fungal biomass

Another set of five leaf discs from each replicate was frozen at −20 °C and used to determine fungal biomass by estimating ergosterol concentrations (Gessner and Chauvet, 1993; Young, 1995). Lipids were extracted from lyophilised and weighed leaf with pentane. After evaporating pentane, the residue was re-dissolved in methanol and ergosterol quantified by high performance liquid chromatography (for details, see Reis et al., 2018). Results were expressed in mg mycelial biomass per g leaf dry mass by the converting of ergosterol into fungal biomass assuming 5.5 μg ergosterol per mg fungal dry mass (Gessner and Chauvet, 1993).

2.4. Microbial respiration

Five leaf discs were immersed in 50 mL Falcon tubes filled with the corresponding O_2 saturated and salted nutrient solution (Jenway 9200 oxygen meter; Jenway, UK). After 16 h in the dark, the final O_2 concentration was measured and leaf discs from each microcosm were removed, oven-dried and weighed. Microbial respiration rates were expressed as mg O_2 consumed g^{-1} DM h^{-1}, where O_2 consumed was determined by the difference between the initial and final measured O_2 concentrations.

2.5. Sporulation rate

At the end of the experiment, an additional five leaf discs of each microcosm were incubated in a 100 mL Erlenmeyer flask containing 25 ml of corresponding salted nutrient solution. After 48 h, conidial suspensions were collected in Falcon tubes and preserved with 2 mL of 37% formalin. Subsamples were filtered (Millipore SMWP, 5 μm pore size, Billerica, MA, U.S.A.) and stained with 0.05% cotton blue in lactic acid (60%), identified and counted at 250× according to Graça et al. (2005). Discs were then oven-dried and weighed to determine final dry mass. Sporulation rates were expressed as the number of spores released per mg DM day^{-1}.

2.6. Statistical analysis

Statistical differences in leaf mass loss, microbial respiration and fungal biomass were determined by two-way Analysis of Variance (ANOVA), to compare each parameter among treatments, with salinity concentration and intermittency regimes as categorical factors. When

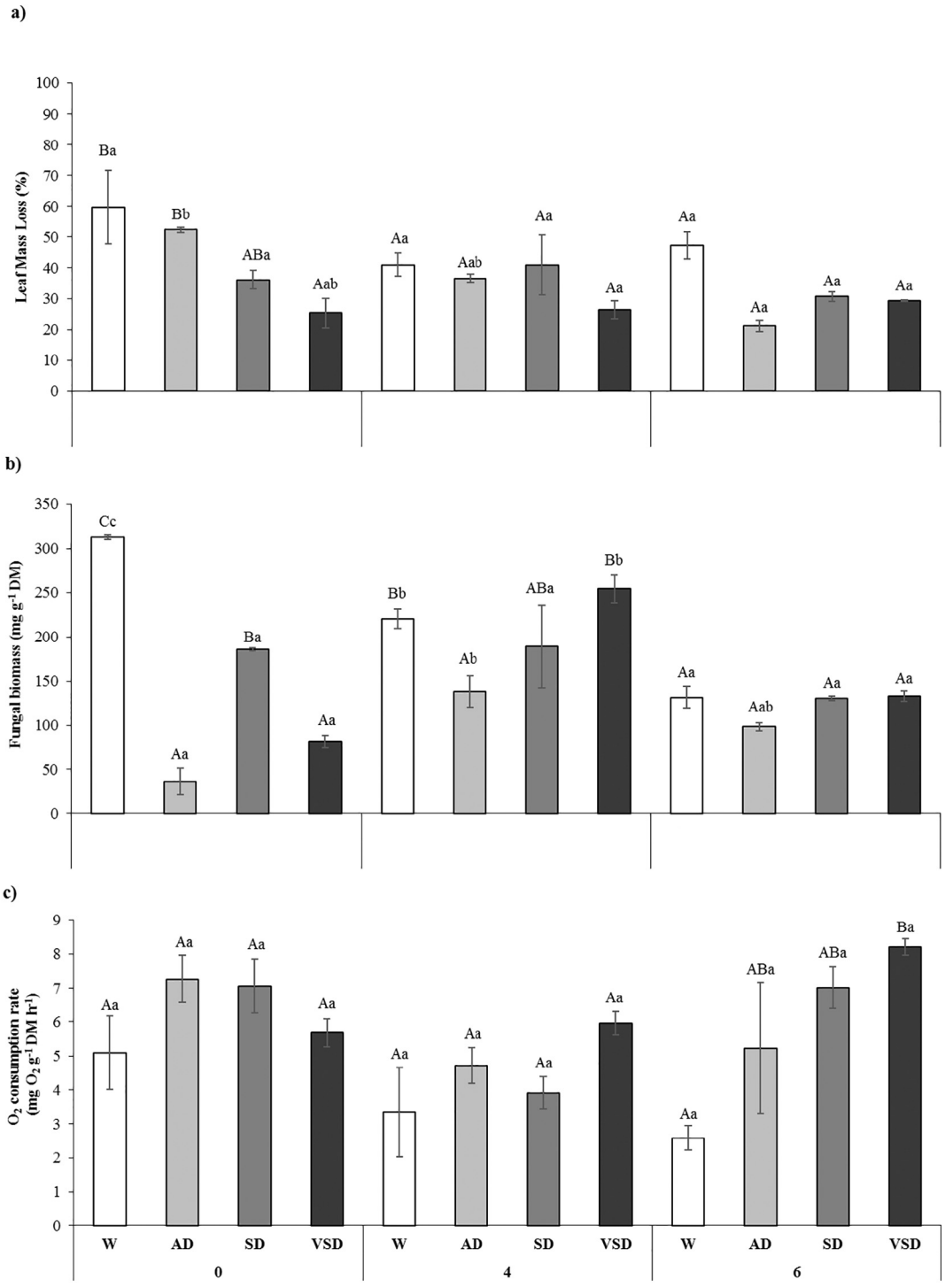

Fig. 2. Leaf mass loss (a), fungal biomass (b) and microbial respiration rates (c) associated with oak leaf discs in microcosms during 10 w (means ± 1SE) under four intermittency regimes (W - wet, AD - abrupt dryness, SD - slow dryness and VSD - very slow dryness) at three salinity concentrations (0, 4 and 6 g L^{-1} NaCl). Bars with different letters indicate significant differences when tested among intermittency (capital letters) or salinity regimes (lowercase letters).

significant statistical differences were observed ($p < 0.05$), planned comparisons were performed to identify the significant effects of one factor within the other and the post-hoc Tukey's test was applied when necessary (as described in the results section). Since no conidia were released in the presence of salt, all sporulation analyses were performed using the data from the reference salinity concentration (=0 g L^{-1}). Therefore, sporulation rates (log (x + 1) transformed) and AH richness were compared among the different intermittency regimes using a one-way ANOVA followed by Tukey's test. Statistical analyses were conducted with STATISTICA 7 software (StatSoft, Tulsa, Oklahoma, USA) and data satisfied assumptions of normality and homoscedasticity. Means (±standard error) presented in the text and figures were calculated using non-transformed data.

Fungal assemblages at different intermittency regimes were compared by a non-metric Multidimensional Scaling (MDS), based on Bray Curtis similarity matrix of log (x + 1) transformed relative abundances of aquatic hyphomycetes conidia (PRIMER 6 & PERMANOVA+; Clarke and Gorley, 2001). Differences among intermittency regimes, under

no salt addition, were also tested by analysis of similarity (one-way ANOSIM).

3. Results

3.1. Leaf mass loss

Permanent regime (W) without salt addition promoted the highest mass loss (59.8% ± 12.0), while the opposite occurred when leaves where subjected to an abrupt drought (AD) at the highest level of salinity (21.1% ± 1.9). Dry mass loss was negatively affected by the exposure of leaves to intermittent flow (two-way ANOVA, $F_{(3, 24)} = 11.59$, $p < 0.001$) and salinity (two-way ANOVA, $F_{(2, 24)} = 6.11$, $p = 0.010$), and it was also affected by the interaction between the two factors (two-way ANOVA, $F_{(6, 24)} = 3.58$, $p = 0.017$). Without salt addition, a more gradual drought induction resulted in lower mass loss (planned comparisons, $F_{(3, 24)} = 11.96$, $p = 0.001$; Fig. 2a), but only VSD leaves decomposed significantly slower than the leaves from the W treatment (Tukey's test, $p = 0.005$). However, in the presence of salt (4 and/or 6 g L^{-1}), the effect of intermittency was attenuated (planned comparisons, $F_{(3, 24)} \geq 2.05$, $p \geq 0.144$). On other hand, the inhibitory effect of salinity on dry mass loss was only significant at AD (planned comparisons, $F_{(2, 24)} = 9.86$, $p = 0.001$) at 6 g L^{-1} of salt (Tukey's test, $p = 0.013$).

3.2. Total fungal biomass

Fungal biomass was significantly affected by both factors (two-way ANOVA, $F_{(3, 24)} = 47.18$ and $F_{(2, 24)} = 31.29$ for intermittency and salinity, respectively, both $p < 0.001$) and their interaction (two-way ANOVA, $F_{(6, 24)} = 22.01$, $p < 0.001$; Fig. 2b). Microcosms inoculated without salt and permanently submerged showed the maximum mycelial biomass (313.2 mg g^{-1} DM ± 2.4). The exposure to desiccation induced a significant reduction of fungal biomass at NaCl ≤ 4 g L^{-1} (planned comparisons, $F_{(3, 24)} \geq 13.04$, $p < 0.001$), with an pronounced decline observed from W to AD treatment (Tukey's test, $p < 0.001$). Increased salinity significantly reduced total fungal biomass present on permanent regime (planned comparisons, $F_{(2, 24)} = 35.71$, $p < 0.001$). Nonetheless, when submitted to intermittency, the fungal biomass was significantly stimulated at the intermediate salinization level (i.e., 4 g L^{-1} NaCl), particularly in AD and VSD conditions (planned comparisons, $F_{(2, 24)} \geq 18.03$, $p < 0.001$).

3.3. Microbial respiration

Microbial respiration was significantly affected by exposure to a drought period (two-way ANOVA, $F_{(3, 24)} = 6.65$, $p = 0.003$), but the only significant affect was found at 6 g L^{-1} of salt (planned comparisons, $F_{(3, 24)} = 11.96$, $p = 0.001$; Fig. 2c), with VSD treatment showing higher respiration rates than W (Tukey's test, $p = 0.016$). Despite the deleterious effect of salinity on oxygen consumption (two-way ANOVA, $F_{(2, 24)} = 4.89$, $p = 0.019$), it was not possible to statistically distinguish among salinity concentrations (planned comparisons, $F_{(2, 24)} = 5.66$, $p \leq 0.012$ at SD; but Tukey's test, $p \geq 0.080$). The interaction between the two main factors, intermittency regimes and salinity, was significant (two-way ANOVA, $F_{(6, 24)} = 2.68$, $p = 0.047$).

3.4. Sporulation

The major impact on conidial production was induced by salinization, given that no conidial release occurred in the presence of salt (i.e., 4 and 6 g L^{-1}). In no salt reference conditions (0 g L^{-1}), when leaves were exposed to drought, sporulation rates were drastically

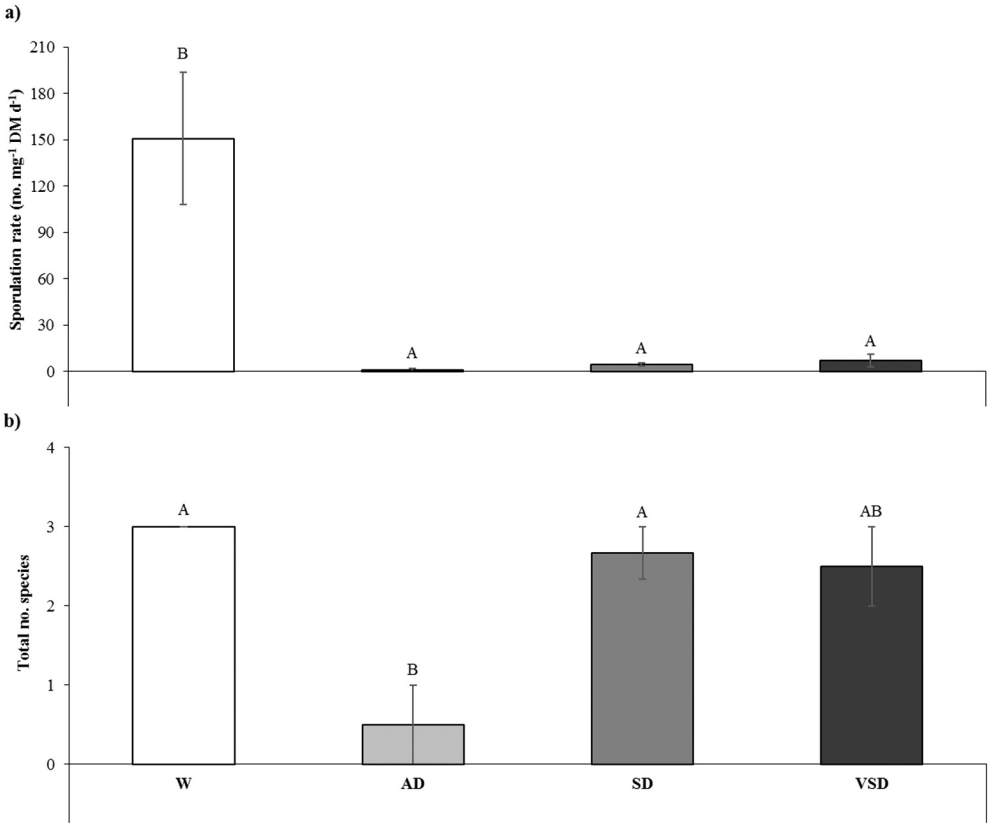

Fig. 3. Sporulation rates (a) and aquatic hyphomycete species (b) associated with oak leaf discs incubated in microcosms during 10w (means ± 1SE) under four intermittency regimes (W - wet, AD - abrupt dryness, SD - slow dryness and VSD - very slow dryness) without salt (0 g L^{-1} NaCl). Bars with different letters indicate significant differences among intermittency regimes.

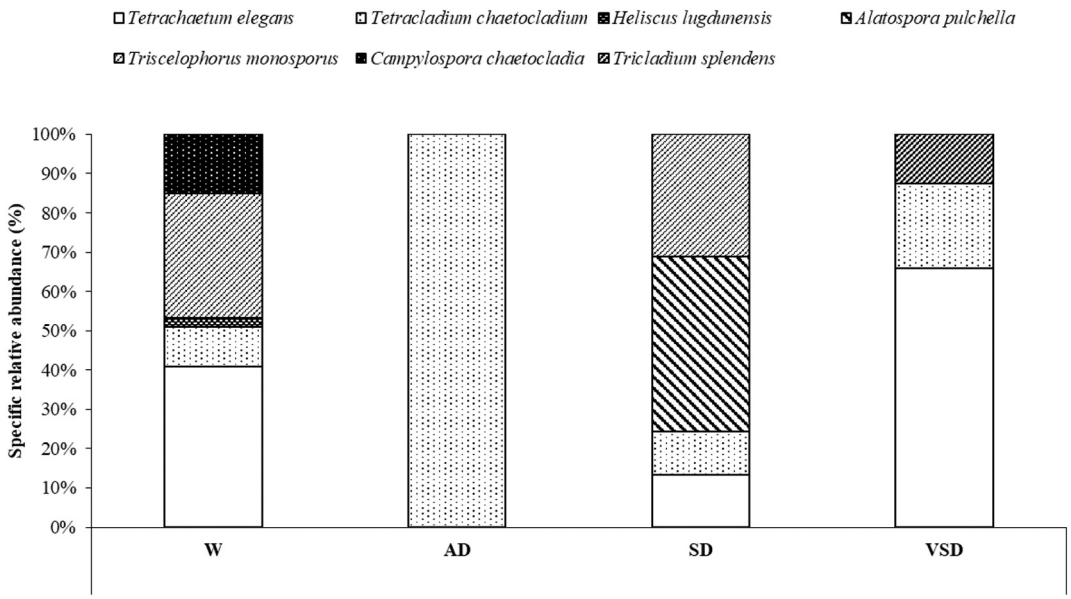

Fig. 4. Mean relative abundances (%) of individual aquatic hyphomycete species in the total conidia associated with oak leaf discs incubated in microcosms during 10 w under four intermittency regimes (W - wet, AD - abrupt dryness, SD - slow dryness and VSD - very slow dryness) without salt (0 g L^{-1} NaCl).

inhibited (~95%) in AD, SD and VSD regimes (≤6.8 conidia mg^{-1} DM d^{-1} ± 4.1; one-way ANOVA, $F_{(3, 8)} = 20.19$, $p = 0.003$; Tukey's test, $p \geq 0.014$; Fig. 3a) in relation to W (150.68 conidia mg^{-1} DM d^{-1} ± 42.79). However, fungal richness was more affected in AD (one-way ANOVA, $F_{(3, 8)} = 7.89$, $p = 0.024$; Tukey's test, $p = 0.027$; Fig. 3b), where just one aquatic hyphomycete species, *Tricladium chaetocladium*, was able to sporulate after drought (Fig. 4). *Tetrachaetum elegans* and *Triscelophorus monosporus* (up to 73% of the total) were the major producers of spores in W regime. At SD, the dominance was shared between *Alatospora pulchella* and *T. monosporus*, while *T. elegans* and *T. chaetocladium* were the main contributors to total conidium production at VSD. The composition of fungal communities associated with oak leaves varied with drought intensity (one-way ANOSIM, $R = 0.506$, $p = 0.011$; Fig. 5), with a dissimilarity between all treatments higher than 67% (essentially promoted by *T. elegans* and *A. pulchella*).

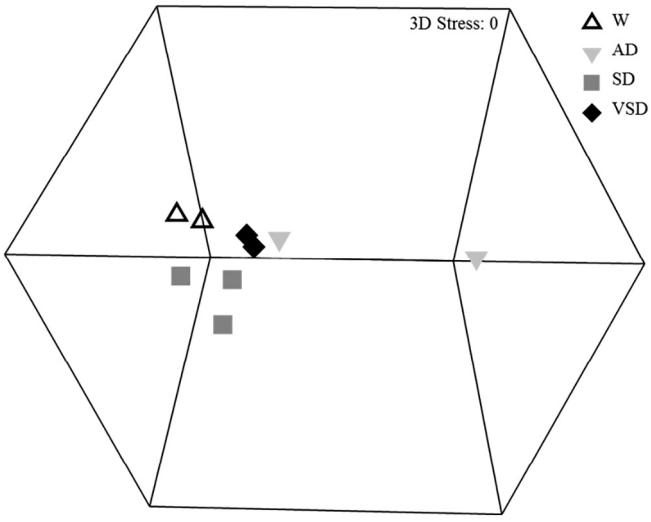

Fig. 5. Non-metric Multidimensional Scaling (3D-NMDS) of oak fungal communities after 10 weeks under four intermittency regimes (W - wet, AD - abrupt dryness, SD - slow dryness and VSD - very slow dryness) without salt (0 g L^{-1} NaCl), based on Bray-Curtis similarity matrix of relative abundances of aquatic hyphomycete conidia.

4. Discussion

Our study corroborates the assumption that salinization can be a dominant stressor in small streams, whose effects may be exacerbated by drought events, particularly at high levels of salt-contamination. The rate of transition between wet and dry conditions has a crucial role in microbial mediated leaf decomposition and consequently for substrate quality fuelling the stream food webs.

Salinization did not affect mass loss of colonized oak leaves or leaf-associated microbial respiration but resulted in a clear reduction of fungal biomass on leaves. These results contrast with most previous studies, which showed a negative relationship between salinization, leaf mass loss (e.g. Schäfer et al., 2012; Swan and DePalma, 2012; Cañedo-Argüelles et al., 2014; Gómez et al., 2016; Sauer et al., 2016) and microbial respiration, even at low salt concentrations (Swan, 2007; Connolly et al., 2014). Recent microcosm studies (Canhoto et al., 2017; Gonçalves et al., 2018), also registered a clear inhibition of leaf degradation and/or oxygen consumption promoted by aquatic hyphomycetes above 4 g L^{-1} NaCl. Although under wet conditions (W) salt-addition per se depressed fungal biomass across all concentrations (as observed in Byrne and Jones, 1975; Sridhar and Kaveriappa, 1988; Schäfer et al., 2012; Cañedo-Argüelles et al., 2014; Gómez et al., 2016; Canhoto et al., 2017; Gonçalves et al., 2018; but see Sauer et al., 2016) this response did not translate into decreased decomposition rates (Gonçalves et al., 2016; Arroita et al., 2018).

The presence of salt completely eliminated the sporulating capacity of the fungal assemblages. This was not surprising considering that conidial production is the most sensitive fungal response to most stressors (Fernandes et al., 2011; Bärlocher et al., 2013; Gonçalves et al., 2016), and that several species have been found to cease sporulation above 2 g L^{-1} NaCl (Canhoto et al., 2017; but see Gonçalves et al., 2018). Overall, it seems plausible that the maintenance of the fungal functional efficiency in salinized environments may be related to energetic trade-offs favouring enzymatic production and mycelial metabolic adjustments at the expense of fungal biomass build up (and sporulation) by tolerant species (Byrne and Jones, 1975; Canhoto et al., 2017; Gonçalves et al., 2018). It has been suggested that tolerance to hyperosmolality may be induced at the cost of the production and accumulation of intracellular organic osmoprotective compounds (Burg and Ferraris, 2008; Canhoto et al., 2017) such as polyols (e.g. glycerol,

erythritol, ribitol, xylitol, sorbitol, galacticol; Kuehn et al., 1998; Burg and Ferraris, 2008). These compounds are involved in the regulation and maintenance of hyphal cell integrity (Hellebust, 1976; Hooley et al., 2003; Overy et al., 2017). Such physiological and metabolic responses have also been proposed to guarantee the decomposer activity of soil microbial communities facing salinity challenges (Asghar et al., 2012). In the present study, all treatments used stream-preconditioned oak leaves (1 w), which guaranteed an initial imprint of fungi and bacteria on the substratum. Although aquatic fungi generally dominate in early stages of decomposition (Findlay et al., 2000; Sridhar and Bärlocher, 2000; Hieber and Gessner, 2002; Gulis and Suberkropp, 2003; Bärlocher, 2005), we cannot rule out the possibility that, under salt stress, the contribution of bacteria to leaf decomposition and microbial respiration across the three salinity levels, in wet treatments, was higher than expected. The potentially compensatory activity of functionally resistant and/or resilient freshwater bacteria (at salt levels between 1.5 and 12 g L^{-1}; Zhang et al., 2014; Berga et al., 2017) could, in fact, have contributed to the apparent contradiction with previous results, which showed an inhibitory effect of salt on fungal-mediated mass loss and respiration (Canhoto et al., 2017; Gonçalves et al., 2018). We predicted that, in the absence of salt, the negative effects of drought on fungal activity would depend on the dryness pattern. We expected that a faster transition to dryness (AD > SD > VSD) would cause greater inhibition of mass loss (Bruder et al., 2011; Arroita et al., 2018). However, despite the corroboration of the deleterious effect of dryness on decomposition (as observed in Bruder et al., 2011; Gonçalves et al., 2016; Duarte et al., 2017; Arroita et al., 2018), our results showed the opposite trend, with the most extreme inhibition of microbial degradative performance occurring at VSD. The previous relationship between fungal biomass and decay rates (Gonçalves et al., 2016; Arroita et al., 2018) was not consistent among treatments, as decreases in fungal biomass (in relation to W) were more pronounced on the most acute (AD = 88.5% reduction) and at the slowest dryness treatment (VSD = 74.0% reduction), with SD inducing a lower reduction (40.7%).

In spite of the well-documented ability of aquatic hyphomycetes to cope with water level fluctuations and to rapidly recover their degradative efficiency (Gonçalves et al., 2016; Arroita et al., 2018), our results showed that an abrupt drought was the only treatment that affected the structure and composition of the fungal communities – only *T. chaetocladium* was able to sporulate after abrupt dryness. Assuming that sporulation is a reasonably reliable indicator of metabolically active aquatic hyphomycete species (Gonçalves et al., 2014; Bärlocher, 2016), the absence of relationship between decomposition rate and fungal parameters (including species number) may indicate that fungal redundancy (Walker, 1992) effectively maintains the functionality of fungal communities in the face of disrupted water flow (as confirmed by Gonçalves et al., 2016). A few, or even a single, desiccation tolerant species, likely taking advantage of decreased or absent competitive interactions, seem able to take over the functions of less tolerant species. These results are in accordance with stream microcosm studies using different stressors (Ferreira and Chauvet, 2012; Geraldes et al., 2012; Gonçalves et al., 2015, 2016), which suggested that individual degradative traits overlap among species present in fungal decomposer assemblages.

In contrast to the AD treatment, conditioned leaves experienced a shorter (SD) or longer (VSD) period of immersion in the ramp drought treatments (sensu Lake, 2000). These are characterized by a period of decreased flow and no turbulence (mimicking stream contraction and pool formation), followed by a moist environment preceding the dry period. A more gradual onset of desiccation may have favoured the persistence of a more diverse, but functionally less comprehensive fungal community. Aquatic hyphomycetes are known to prefer well-aerated and turbulent aquatic environments (Medeiros et al., 2009; Canhoto et al., 2013) although they may remain active on leaves in lentic and even moist environments (Baldy et al., 2002; Chauvet et al., 2016). This capacity, possibly maintained by species-specific osmoprotective responses against desiccation (Baumann and Marschner, 2013), may occur at the expenses of fungal biomass production and leaf decomposition rates (Gonçalves et al., 2016).

Ramp droughts scenarios (particularly in VSD), may also favour prokaryotic microorganisms that benefit from extended stagnant and therefore less oxygenated conditions contributing to overall leaf degradation upon resumption of water flow. Keeping in mind differences in the experimental systems, it is interesting to note that Pérez et al. (2018) also registered decreased fungal:bacterial ratios under longer wet:dry periods (28 to 56 days of drought, which was similar to our dry period), in a study of tank bromeliads. In fact, microbial respiration did not differ among the drought treatments despite differences in fungal biomass; this apparent discrepancy may be related to an increased bacterial contribution to global O_2 consumption due to higher biomass (especially in VSD) and/or to species-specific differences in ergosterol concentrations (proxy of fungal biomass) and/or metabolic activity between fungal species (Gessner and Chauvet, 1993; Gonçalves et al., 2014).

Overall our results support previous findings that direct impact of salinization at 4 and 6 g L^{-1} on the degradative efficiency of fungi may be relatively low, while abrupt, long-lasting droughts in highly salinized streams may precipitate a critical reduction of fungal diversity, either in terms of species richness or through changes in community structure. It reinforces the observation that in the presence of multiple stressors, synergistic or antagonistic effects on species and community responses are common (e.g., nutrients and flow regulations on fungal communities; Noel et al., 2016). This impairs our ability to predict consequences of the combined effects of two or more stressors. Nevertheless, it is reasonable to assume that if the species most sensitive to at least one of the tested stressors are also functionally more effective, the impact on leaf litter decomposition will be exacerbated. Ultimately, effects on leaf litter quality in terms of fungal diversity and biomass may impair leaf incorporation into secondary production (Canhoto and Graça, 2008; Gonçalves et al., 2014). More gradual drought events in salinized streams will likely affect ecosystem functioning primarily through effects on litter conditioning. It will modify fungal biomass accrual and nutrient status due to a possible increase in bacterial biomass and activity. It is generally accepted that invertebrates prefer fully fungal-conditioned leaves, that shredders consistently prefer and consume conditioned over unconditioned leaf material, and that they often select material conditioned by specific aquatic hyphomycete species (Canhoto and Graça, 2008; Gonçalves et al., 2014). Therefore, a disruption on the dynamics of detrital food webs in streams through fungal diversity losses and/or biomass reduction can be expected in intermittent salinized streams. The specific effects of this disruption will depend on the temporal patterns of drying and the severity of drought events. Future investigations about the impacts of anthropogenic environmental fluctuations on structure and function of aquatic ecosystems (particularly on decomposer fungi and bacteria) should include more tests on the effects of the magnitude and frequency of salt and intermittency conditions, of particular relevance in semi-arid and Mediterranean areas where both stressors are more concomitant. This may provide more reliable information on the combined effects of both stressors, facilitate guidance for environmental water management and suggest practices and strategies that reduce salinization and sustain water resources (Cañedo-Arguelles et al., 2016).

Competing interests

We have no competing interests.

CRediT authorship contribution statement

Ana Lúcia Gonçalves: Conceptualization, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Sara Simões:** Investigation, Writing - review & editing. **Felix Bärlocher:** Conceptualization,

Writing - review & editing. **Cristina Canhoto:** Conceptualization, Writing - review & editing.

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